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Modality-independent effect of gravity in shaping the internal representation of 3D space for visual and haptic object perception

Abbreviated title:

Gravity's effect on internal representation of space

Theo Morfousse^{1,#}, Gabriela Herrera Altamira^{1,#}, Leonardo Angelini^{2,3}, Gilles Clément⁴, Mathieu Beraneck¹, Joseph McIntyre^{1,5}, Michele Tagliabue^{1*}

These authors contributed equally

- 1 Université Paris Cité, CNRS UMR 8002, INCC - Integrative Neuroscience and Cognition Center, F-75006, Paris, France.
- 2 HumanTech Institute, University of Applied Sciences Western Switzerland//HES-SO, 1700 Fribourg, Switzerland
- 3 School of Management Fribourg, University of Applied Sciences Western Switzerland//HES-SO, 1700 Fribourg, Switzerland
- 4 Université de Caen Normandie, Inserm, COMETE U1075, CYCERON, CHU de Caen, Normandie Univ, 14000, Caen, France.
- 5 Tecalia, Basque Research and Technology Alliance, 20009, San Sebastian, Spain

* **Corresponding author:** Michele Tagliabue; 45 rue des St-Pères; Université Paris Cité, Integrative Neuroscience and Cognition Center, CNRS UMR 8002, F-75270 Paris, France. E-mail: michele.tagliabue@parisdescartes.fr

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Abstract

Visual and haptic perceptions of 3D shape are plagued by distortions, which are influenced by non-visual factors, such as gravitational vestibular signals. Whether gravity acts directly on the visual or haptic systems or at a higher, modality-independent level of information processing remains unknown. To test these hypotheses, we examined visual and haptic 3D shape perception by asking male and female human subjects to perform a “squaring” task in upright and supine postures and in microgravity. Subjects adjusted one edge of a 3D object to match the length of another in each of the 3 canonical reference planes and we recorded the matching errors to obtain a characterization of the perceived 3D shape. The results show opposing, body-centered patterns of errors for visual and haptic modalities, whose amplitudes are negatively correlated, suggesting that they arise in distinct modality-specific representations that are nevertheless linked at some level. On the other hand, weightlessness significantly modulated both visual and haptic perceptual distortions in the same way, indicating a common, modality-independent origin for gravity’s effects. Overall, our findings show a link between modality-specific visual and haptic perceptual distortions and demonstrate a role of gravity-related signals on a modality-independent internal representation of the body and peripersonal 3D space used to interpret incoming sensory inputs.

Significance Statement

Both visual and haptic 3D-object perception are plagued by anisotropic patterns of errors, as shown in a task of “squaring” the faces of an adjustable cube.

We report opposing and negatively correlated perceptive errors for the visual and haptic perceptions, suggesting a strong interaction between the two sensory modalities, even when the task was fundamentally unimodal.

In addition, the similar effect of microgravity observed on both visual and haptic perception indicates that gravity acts on a modality-independent representation of 3D space used to process these sensory inputs.

These findings foster awareness that even simple, unimodal, egocentric tasks are likely to involve complex, cross-modal signal processing.

61 Introduction

62 Perception of three-dimensional (3D) objects includes the ability to determine an item's location
63 in space, as well as its geometrical properties, such as the relative size along each of three
64 dimensions and the relative orientation of its edges. Given its importance for interacting with the
65 physical world, 3D object perception has been deeply investigated. Visual perception has received
66 the most attention, showing how various features of the stimuli, such as disparities, size,
67 occlusions, perspective, motion, shadows, shading, texture and blur, all influence 3D visual
68 perception (Welchman, 2016) and how *internal models* shape the interpretation of the sensory
69 signals (Curry, 1972; Kersten and Yuille, 2003; Kersten et al., 2004; Lee, 2015).

70 Despite its critical importance to perception and action, visual perception suffers from measurable
71 distortions: i.e. height underestimation with respect to width, also known as the horizontal-
72 vertical, or "L", illusion (Avery and Day, 1969) and a systematic underestimation of depth (Loomis
73 and Philbeck, 1999; Todd and Norman, 2003). Non-visual factors, such as gravity, also appear to
74 affect visual perception. For example, tilting the body with respect to gravity affects object
75 recognition (Leone, 1998; Barnett-Cowan et al., 2015), orientation and distance perception
76 (Marendaz et al., 1993; Harris and Mander, 2014), and other phenomena such as the tilted frame
77 illusion (Goodenough et al., 1981; Howard, 1982), the oblique effect (Lipshits and McIntyre, 1999;
78 Luyat and Gentaz, 2002; McIntyre and Lipshits, 2008) and some geometric illusions (Prinzmetal
79 and Beck, 2001; Clément and Eckardt, 2005). Furthermore, weightlessness significantly alters the
80 perception of stimulus size and shape, especially in tasks involving depth, during both short-term
81 (Villard et al., 2005; Clément and Buckley, 2008; Clément et al., 2008; Harris et al., 2010; Clément
82 and Demel, 2012; Clément et al., 2016; Bourrelly et al., 2016) and long-term (Clément et al., 2012,
83 2013; De Saedeleer et al., 2013; Bourrelly et al., 2015) exposure.

84 One hypothesis to explain gravity-related changes in visual perception is that gravity affects both
85 the eye movements underlying visual exploration (Clément et al., 1986; Reschke et al., 2017,
86 2018) and eye positioning that contributes to the estimation of the visual eye-height, a key
87 reference within the visual scene (Goltz et al., 1997; Bourrelly et al. 2016). Gravity's influence on
88 oculomotor control should specifically affect visual perception, although weightlessness might

also induce distinct distortions in other sensory modalities. An alternative hypothesis is that gravity does not affect visual signals *per se*, but rather affects an internal representation of space (Clément et al., 2009, 2012), based on prior knowledge, that serves to interpret those signals, independent of the sensory system from which they come (Wolbers et al., 2011; Loomis et al., 2013). An example, among many, of the use of an internal model of space for perception is the famous ‘Ames room’ illusion, where persons’ size is misperceived due to the use of the inappropriate prior that the room is rectangular (O'Reilly et al., 2012). A direct implication of this second hypothesis is that microgravity should distort all spatial perceptions in the same way, regardless of the sensory modality. Because previous studies in microgravity were focused on visual tasks only, however, these proposed hypotheses have never been tested.

To investigate these two assumptions, we first compared distortions of visual versus haptic perception of 3D shape in a normal, upright posture on Earth. Next, we studied the effect of changing the subject’s orientation with respect to gravity to assess whether any visual or haptic distortions are egocentric or gravity-centric. Third, we tested the consequences of removing the effects of gravity by performing both haptic and visual experiments in weightlessness during parabolic flight.

Materials and Methods

In an analogy with previous experiments on visual perception (Clément et al., 2008, 2013), our paradigm was conceptually designed to detect distortions in the perception of three-dimensional shape, i.e., the relative lengths of the sides of a 3D cube. The sequential nature of haptic perception induced us, however, to focus each trial on the comparison of the relative size between two out of three possible dimensions. In both the visual and the haptic cases, the task consisted of adjusting one side of the rectangle to match the other, to form a square. The adjustments were performed using a trackball held in the left hand. In the haptic task the right hand was used to explore the rectangle. Subjects pressed a button on a trackball when they perceived the object to be perfectly square.

For the haptic tasks, subjects were asked to close their eyes and to feel, through haptic sense only, a rectangular cutout in a rigid, virtual plank generated by a Force Dimension Omega.3 haptic

117 robot (Figure 1A). This manipulandum was able to simulate the presence of a 3D object by
118 applying the appropriate contact forces on the right hand of the subject when he/she performed
119 exploration movements aimed at perceiving its shape and size. During each trial the robot
120 constrained the subject's hand movement to lie within the plane of the virtual plank and to
121 remain inside the rectangle prescribed by the virtual cutout. To allow direct comparisons
122 between the experimental results from haptic and visual tests, an analogous bi-dimensional task
123 was also used for visual perception. Subjects were shown planar rectangles with different
124 orientations in 3D space, without being able to manually explore it. For trials involving visual
125 perception, an Oculus Rift virtual reality headset was used to provide a stereoscopic view of the
126 virtual object. The visual environment was dark and the shapes were represented by light-gray
127 frames. For both sensory conditions, the virtual object was located approximatively 40 cm in front
128 of the subject's right shoulder.

129 Although there were no instructions to work quickly, subjects were asked to attempt to perform
130 each trial in a fixed time window (20 s for all experiments except those performed on board the
131 parabolic flight plane, for which a 10 s time window was used). An audible cue indicated to the
132 subject when the end of the allotted time was approaching. The apparatus recorded the subject's
133 final responses (dimensions of each rectangle judged to be square), which is the main output of
134 the tests. For the haptic tasks, the movements of the subject's hand and the contact forces applied
135 against the virtual constraints were also recorded via the haptic device.

136 The use of two-dimensional tasks allowed the estimation of the perceptive error in one plane at
137 a time. Subjects in our experiments judged the squareness of rectangles lying in each of three
138 anatomical planes: frontal, sagittal, or transversal (see bottom part of Figure 1A). The combination
139 of the three possible planes and the two rectangle dimensions resulted in six different geometric
140 configurations that the subject had to deal with. They are represented in the upper part of Figure
141 2. At the beginning of each trial, an audio command told the subject in which anatomical plane
142 the rectangle was lying and which of the two dimensions of the rectangle had to be adjusted. In
143 our paradigm, the reference dimension was always 40 mm, but subjects were not informed of this
144 fact. The initial length of the adjustable side was randomly selected between 15, 25, 35, 45, 55,
145 and 65 mm. Subjects performed five series of trials in all; each series being composed of a random

146 permutation of the six geometric configurations (total number of trials per condition: 30). In all
147 three experiments described below, each subject was tested in two different conditions, so that
148 in total each subject performed 60 trials. The two conditions, which depended on the experiment,
149 were tested successively and their order was counterbalanced (half of subjects started with
150 condition 1 and the other half with condition 2).

151

152 [Figure 1 about here]

153

154 **Experiment 1: Effect of Sensory Modality**

155 To study the differences and similarities between haptic and visual perception of 3D shapes in
156 normo-gravity, 18 seated subjects (8 males, 10 females, aged 29 ± 9) performed the task for all six
157 geometrical configurations in each of the two sensory conditions: Haptic and Visual. The order
158 of the two sensory conditions was randomized across subjects.

159 **Experiment 2: Effect of Body Orientation**

160 To study the perceptive distortions of both haptic and visual senses and whether the information
161 is encoded in an egocentric (body-centered) or allocentric (gravity-centered) reference frame, a
162 group of 18 subjects (9 males and 9 females, aged 25.5 ± 5 years) performed the haptic task while
163 seated (Upright) and while lying on the back (Supine), while a second group of 18 subjects (11
164 male and 7 female, aged 24 ± 4 years) performed the visual task in the same two postures (Upright
165 and Supine). For the Supine posture, subjects lied on a medical bed. The two postures are repre-
166 sented in Figure 2 together with the respective correspondence between egocentric and
167 allocentric references. The virtual object was placed always at the same distance from the subject's
168 shoulder, independent of the posture. In order to compensate for possible learning effects, the
169 order of the postural conditions was randomized in both sensory conditions.

170

171 [Figure 2 about here]

172

173 **Experiment 3: Effect of Weightlessness**

174 To study the role of gravitational cues in the encoding of haptic and visual signals we performed
175 the haptic (18 subjects: 10 males, 8 females, aged 38 ± 11 years) and visual (18 subjects: 9 males, 9
176 females, aged 41 ± 11 years) paradigm in normal gravity (1G) and during the weightlessness phases
177 of parabolic flight (0G). For the haptic experiment, a third condition was added: the subjects were
178 also tested in normal gravity, but with the arm supported by a strap (Supp.), to differentiate the
179 biomechanical effect of gravity on the arm from the gravitational stimulation of graviceptors,
180 such as the otoliths.

181 Parabolic flight provides short intervals (~ 20 s) of weightlessness within a stable visual
182 environment inside the airplane, bracketed by periods of hyper-gravity (1.6 - 1.8 G) just before
183 and just after each period of weightlessness. Given the short duration of 0G phases during
184 parabolic flight, the subjects were trained to perform the task in about 10 seconds (two tasks per
185 parabola). Since each subject performed the experiment during 15 consecutive parabolas, he or
186 she could perform all 30 trials per condition.

187 All experimental conditions were performed inflight onboard the Novespace Zero-G airplane in
188 order to minimize possible undesired changes in uncontrolled factors. The 1G and Support
189 conditions were tested during the level-flight phase just preceding the first parabola or just
190 following the last parabola of its session, depending on the subject. The subjects were very firmly
191 restrained with belts so that their relative position with respect to the apparatus and the virtual
192 rectangles did not vary between gravitational conditions.

193 **Ethical approval**

194 The experimental protocols of experiment 1 and 2 performed at Université Paris Cité were
195 approved by the university review board "Comité Éthique de la Recherche" CER (approval
196 number 2016/33). The experiments performed on board of the Zero-G airplane were approved
197 by the French national ethic committee "Comité de Protection des Personnes", CPP (approval
198 number: 2014-A01949-38)

Data analysis

For each trial, t , the error, ε , between the length of the adjustable and reference sides of the rectangle was computed. If the egocentered definition of the three dimensions (Lateral, LA ; Longitudinal, LO ; Anterior-Posterior, AP) of Figure 1B is used, the errors of the six geometric configurations are defined as $LA-LO$, $LO-LA$, $LA-AP$, $AP-LA$, $LO-AP$, and $AP-LO$, where the minuend and subtrahend are the adjustable and reference dimensions respectively.

[Table 1 about here]

Table 1 shows how the perceptive distortion associated with each of the three dimensions contributes to the error made on the six geometric configurations. Positive errors correspond to underestimations of the adjustable dimension and/or to overestimations of the reference dimension. Thus, the present experimental paradigm, similar to the one previously used by Clément et al. (2008, 2013), allows the quantification of the perceptive errors of one dimension relative to another, but cannot lead to a measure of the absolute perceptive errors for each dimension separately.

Estimation of 3 orthogonal perceptual errors

Table 1 shows that the error in estimating one dimension has opposite effects for the two tasks performed within a given plane. For instance, an overestimation of the AP dimension should result in negative and positive errors in the AP-LA and LA-AP tasks, respectively. These relationships appear to be confirmed by the experimental results (Figure 4A), because this hypothesis accounts for 96% of the data variance. It follows that the theoretical relationships below are valid:

$$\begin{aligned}\varepsilon_{LA-AP} &= -\varepsilon_{AP-LA} \\ \varepsilon_{LA-LO} &= -\varepsilon_{LO-LA} \\ \varepsilon_{LO-AP} &= -\varepsilon_{AP-LO}\end{aligned}\tag{1}$$

Exploiting this property, it was possible to combine the five errors obtained for one geometric condition, with the additive inverse of the five errors obtained for the other geometric condition performed in the same plane. This allowed computing the combined mean and the variance of the errors for each of the three planes (Transverse, *Tra*; Frontal, *Fro*; Sagittal, *Sag*), instead of individually for each of the 6 geometrical configurations of the task. This technique has the considerable advantage of being more robust, because it is based on 10 samples instead of only 5.

$$\begin{aligned}
 \bar{\varepsilon}_{Tra} &= \frac{\sum_{t=1}^5 (\varepsilon_{LA-AP,t} - \varepsilon_{AP-LA,t})}{10} \\
 \sigma_{Tra}^2 &= \frac{\sum_{t=1}^5 ((\varepsilon_{LA-AP,t} - \bar{\varepsilon}_{Tra})^2 + (-\varepsilon_{AP-LA,t} - \bar{\varepsilon}_{Tra})^2)}{10} \\
 \bar{\varepsilon}_{Fro} &= \frac{\sum_{t=1}^5 (\varepsilon_{LA-LO,t} - \varepsilon_{LO-LA,t})}{10} \\
 \sigma_{Fro}^2 &= \frac{\sum_{t=1}^5 ((\varepsilon_{LA-LO,t} - \bar{\varepsilon}_{Fro})^2 + (-\varepsilon_{LO-LA,t} - \bar{\varepsilon}_{Fro})^2)}{10} \\
 \bar{\varepsilon}_{Sag} &= \frac{\sum_{t=1}^5 (\varepsilon_{AP-LO,t} - \varepsilon_{LO-AP,t})}{10} \\
 \sigma_{Fro}^2 &= \frac{\sum_{t=1}^5 ((\varepsilon_{AP-LO,t} - \bar{\varepsilon}_{Sag})^2 + (-\varepsilon_{LO-AP,t} - \bar{\varepsilon}_{Fro})^2)}{10}
 \end{aligned} \tag{2}$$

With the above formulas, one can characterize perceptual distortions in each of the three different planes as illustrated in Figure 3. By our convention, a rectangle lying in one of the two vertical planes (Sagittal or Frontal) is associated with a positive error (stubby rectangle) if the longitudinal dimension is smaller than the other dimension. In the transverse plane, a positive error (stubby rectangle) corresponds to the AP dimension being smaller than the LA dimension. It is worth noting that if the subject produced a “stubby” rectangle (positive errors) this means that he/she perceived a square to be “slender”, and vice versa. The global variance was computed as the average of the three planar variances.

237

238 [Figure 3 about here]

239

240 The estimation of the three planar errors is then improved by considering that if the (distorted)
241 metrics used to compare distances in 3D space are locally smooth and consistent for the different
242 dimensions in space, the three planar errors ε are not independent and that, given the sign
243 conventions of Figure 3, they should fulfill the following relationship

$$\bar{\varepsilon}_{Sag} + \bar{\varepsilon}_{Tra} = \bar{\varepsilon}_{Fro} \quad (3)$$

244 Note that equation 3 is a particular case of the formula describing a plane, $ax + by + cz = d$, where
245 $a = b = 1$, $c = -1$ and $d = 0$. Thus, if the metrics in each plane are consistent with each other, the
246 vectors of measured planar errors $\bar{\varepsilon} = [\bar{\varepsilon}_{Sag} \ \bar{\varepsilon}_{Tra} \ \bar{\varepsilon}_{Fro}]$ should fall on that plane and points outside
247 the plane can be considered to be noise. By projecting the individual vectors $\bar{\varepsilon}$ onto the plane
248 corresponding to equation 3 as shown in Figure 4A-B, this noise is effectively filtered out. Using
249 the resulting 2D representation of the distortion (Figure 4C) is a conservative choice, especially
250 when comparing their orientation in different conditions, because the 3D representation may
251 lead to consider distortion directions and components of data variability that have no functional
252 meaning. On average, the data projected on the plane of equation 3 account for 98% of the
253 variance of the original data, suggesting that the recorded responses tend to well fulfill this
254 constraint.

255

256 [Figure 4 about here]

257

258 We used the same equations (1-3) to compute the analogous parameter in the allocentric
259 reference frame after having replaced the egocentrically defined planes and directions with the
260 world-centered planes (Horizontal, *Hor*; Latitudinal, *Lat*; Meridian, *Mer*) and directions (*East-*
261 *West*, *North-South*, and *Up-Down*) as shown in Figure 2. Table 2 shows the relationships
262 between the planar distortions defined in the body-centered and gravity-centered reference
263 frame for the Upright and Supine posture.

264

Perceptive cuboids

Although, as stated before, the present experimental paradigm, does not allow a measure of the absolute perceptive errors for each dimension separately, we have devised a methodology that allows one to visualize the 3D patterns of distortion as a “perceptive cuboid”, that is an elongated box compared to an ideal undistorted cube. To compute the dimensional errors, we first solved the system of equations of Table 1 reported below in the matrix form.

$$\begin{bmatrix} \varepsilon_{LA-LO} \\ \varepsilon_{LO-LA} \\ \varepsilon_{LA-AP} \\ \varepsilon_{AP-LA} \\ \varepsilon_{LO-AP} \\ \varepsilon_{AP-LO} \end{bmatrix} = A \cdot \begin{bmatrix} \varepsilon_{LA} \\ \varepsilon_{AP} \\ \varepsilon_{LO} \end{bmatrix} = \begin{bmatrix} 1 & 0 & -1 \\ -1 & 0 & 1 \\ 1 & -1 & 0 \\ -1 & 1 & 0 \\ 0 & -1 & 1 \\ 0 & 1 & -1 \end{bmatrix} \cdot \begin{bmatrix} \varepsilon_{LA} \\ \varepsilon_{AP} \\ \varepsilon_{LO} \end{bmatrix}$$

If we call A the matrix of linear coefficient, then the solutions of this underdetermined problem are

$$\begin{bmatrix} \varepsilon_{LA} \\ \varepsilon_{AP} \\ \varepsilon_{LO} \end{bmatrix} = A^\dagger \cdot \begin{bmatrix} \varepsilon_{LA-LO} \\ \varepsilon_{LO-LA} \\ \varepsilon_{LA-AP} \\ \varepsilon_{AP-LA} \\ \varepsilon_{LO-AP} \\ \varepsilon_{AP-LO} \end{bmatrix} + (I - A^\dagger A) \cdot \begin{bmatrix} \varepsilon_{LA} \\ \varepsilon_{AP} \\ \varepsilon_{LO} \end{bmatrix} = A^\dagger \cdot \begin{bmatrix} \varepsilon_{LA-LO} \\ \varepsilon_{LO-LA} \\ \varepsilon_{LA-AP} \\ \varepsilon_{AP-LA} \\ \varepsilon_{LO-AP} \\ \varepsilon_{AP-LO} \end{bmatrix} + (I - A^\dagger A)w = A^\dagger \cdot \begin{bmatrix} \varepsilon_{LA-LO} \\ \varepsilon_{LO-LA} \\ \varepsilon_{LA-AP} \\ \varepsilon_{AP-LA} \\ \varepsilon_{LO-AP} \\ \varepsilon_{AP-LO} \end{bmatrix} + \begin{bmatrix} w \\ w \\ w \end{bmatrix}$$

Where the A^\dagger is the pseudo inverse of A and w is a free scalar parameter that reflects the fact that the observed results can be explained by an infinity of triplets of dimensional distortions differing by isotropic component, w , only (underdetermination of the problem).

To define a set of dimensional errors, $(\varepsilon_{LA}, \varepsilon_{AP}, \varepsilon_{LO})$ to be used for a graphical representation, we arbitrary decided to select the solution that minimizes the Euclidean norm of the error vectors.

Although the w parameter cannot be univocally defined, the difference between the errors along the three dimensions are correctly quantified and then used to test the anisotropy of the perceptive errors. The dimensional errors, however, cannot be rigorously compared between postures or gravitational conditions, because the differences between experimental conditions could be due to differences in defining the w parameter for each condition.

287 **Polar representation of errors**

288 The 2D vector resulting from the projection of $\bar{\epsilon}$ to the plane of equation 3 was computed for
289 each subject (Figure 4C) and represented with a polar plot. The vector length corresponds to the
290 Euclidian sum of the filtered error triplets and its direction provides information about the
291 “shape” of the pattern of errors, meaning the relative magnitude and sign of the errors in the
292 three anatomical planes: a pattern of errors restricted to an expansion or contraction along the
293 anterior-posterior axis, with no errors in the fronto-parallel plane will give a vector pointing
294 along the 0° or 180° axes, respectively; a pattern of errors restricted to a contraction or expansion
295 along the lateral axis, with no errors in the sagittal plane corresponds to a vector with a 60° or
296 240° orientation, respectively; a pattern of errors that is restricted to an expansion or contraction
297 in the longitudinal direction, with no distortion between the axes in the transversal plane will
298 give a vector that points along the 120° or 300° axes in the polar plot, respectively. Vectors that
299 point along intermediate angles indicate more complex patterns wherein an over-estimation
300 along one anatomical axis and an underestimation along another axis are combined (e.g. the 30°
301 orientation corresponds to AP and LA dimensions that are respectively over-estimated and
302 underestimated compared to LO).

303 The strength of the misalignment, Mis , between the individual 2D vectors representing the two
304 conditions tested in an experiment, was computed as the cross-product of the two individual
305 vectors. The value of Mis , which, as illustrated in Figure 4D, corresponds to the area of the
306 parallelogram having the two vectors as adjacent sides, is zero when the two vectors are in the
307 same, or opposite, direction and maximal when they are orthogonal. Importantly, Mis amplitude
308 depends also on the vectors’ lengths, so that the Mis value associated to long vectors is larger than
309 for short vectors for the same amount of misalignment. This gives a desired feature that large
310 vectors, which have a well-defined direction, are given greater weight in statistical analyses than
311 small vectors whose direction can be significantly deviated by experimental noise.

312 In each experimental condition, the vectorial mean of the 2D individual vectors was computed
313 to represent the average perceptive error.

314 **Reaction forces during haptic task**

315 To estimate changes of the contact forces between gravitational conditions in the haptic tasks,
316 we computed the average of the reaction forces generated by the haptic device when the subject's
317 hand was in contact with the edges of the virtual cutout or when the hand tried to move out of
318 the task plane.

319 **Microgravity effect and theoretical prediction**

320 To quantify the effect of microgravity on the perceptive errors, for each subject, s , the mean
321 planar error in 1G was subtracted from the corresponding error in 0G:

$$322 \quad \Delta \bar{\epsilon}_s = \bar{\epsilon}_{s,0G} - \bar{\epsilon}_{s,1G}$$

323 To predict the perceptive distortion expected in microgravity under the hypothesis that the 0G
324 effect was identical for the haptic and visual modalities, we averaged all error triplets $\Delta \bar{\epsilon}_s$
325 representing the measured individual microgravity effects from both the haptic and visual
326 experiments (18 haptic subjects, 18 visual subjects):

$$327 \quad \Delta \bar{\epsilon} = \frac{\sum_{s=1}^{36} \Delta \bar{\epsilon}_s}{36}$$

328 The obtained average triplet was then added to the individual visual and haptic errors measured
329 in normo-gravity conditions to compute the predicted error in microgravity, $\hat{\epsilon}_{s,0G}$.

$$330 \quad \hat{\epsilon}_{s,0G} = \bar{\epsilon}_{s,1G} + \Delta \bar{\epsilon}$$

331 We then compared these individual predictions to the errors measured in 0G for both visual and
332 haptic modalities, to see to what extent a common mechanism for visual and haptic captures the
333 data.

334 **Statistical analysis**

335 For each experiment, we first tested the significance of the squaring errors by testing for each
336 plane whether the constant errors were on average different from zero (two-sided Student's t-
337 test). Then, we performed repeated-measures ANOVA on the constant and variable errors. The
338 sign conventions (Figure 3) being arbitrary, they allow a rigorous comparison of the errors within
339 a given plane, but they do not allow the comparison between different planes. For this reason, in

the statistical analyses, the results on each plane were tested with independent ANOVAs for repeated measures.

Experiment 1: For each of the 3 task planes we tested for an effect of Sensory Modality on the perceptive error as a single within-subject independent factor with two levels (Haptic, Visual).

Experiment 2: We tested for an effect of Body Posture as a within-subject independent factor with two levels (*Upright*, *Supine*) in separate ANOVAs for each group/sensory modality (Visual and Haptic). Note that this separation is justified by the hypotheses being tested, for which cross effects between posture and modality would have little meaning. To test whether errors are tied to a body-centric or gravity-centric reference frame, we defined the task planes both in terms of anatomical axes and world axes. Invariance of pattern of error (lack of a statistical difference) for the anatomically defined planes, but not the world-defined frames, would indicate that the errors are primarily egocentrically, rather than allocentrically, aligned.

Experiment 3: For each of the 3 task planes we tested for an effect of Gravity on the squaring error as a single within-subject independent factor with three (1G, 0G, Supported) and two (1G, 0G) levels for the haptic and visual experiment respectively.

Before performing each ANOVA, we tested for normality and homogeneity of the distributions using the Kolmogorov-Smirnov and Levenes tests, respectively. To achieve the normal distribution for the response variability, the standard deviations were transformed by the $\log(\sigma+1)$ function (Tagliabue and McIntyre 2011). For the errors expressed in both allocentric and egocentric reference frames the data were distributed normally (all $p>0.20$) and the data variability was similar among all conditions (all $p>0.50$).

In order to test whether the variability of the individual squaring errors in the haptic modality can explain the errors in the visual modality (and vice versa), their coefficient of correlation R , with the relative p-value, was computed.

Because the *Mis* parameter did not always show a normal distribution, it is presented in terms of median \pm inter-quartile range and a non-parametric Sign Test was used to test whether its distribution is significantly different from zero.

368 To test whether the pattern of errors (2D vectors) differs between two conditions (experiment 1:
 369 visual vs haptic; experiments 2: upright vs supine; experiments 3: 1G vs 0G), a bootstrap technique
 370 was used. This technique, which allows one to correctly take into account both direction and
 371 amplitude of the individual vectors, consisted of using 10000 re-samplings with replacement of
 372 the 18 subjects to estimate the statistical distribution of the difference in amplitude, ΔAmp , and
 373 the angle, θ , between the vectorial average of two conditions, and to compute the probability of
 374 error in rejecting the null hypothesis, H_0 , that $\theta=0$. Following a Bayesian approach, taking into
 375 account a prior uniform distribution of all possible angles (θ range $\pm 180^\circ$), we evaluated the ratio,
 376 $R_{0/1}$, between the probability to obtain the observed data under the null hypothesis, H_0 , and the
 377 probability under the alternative hypothesis, H_1 , that $\theta \neq 0$ (Wagenmakers et al., 2018).

378 In experiment 3, to test whether the effect of microgravity has the same direction for visual and
 379 haptic modalities the bootstrap re-sampling was performed independently for the two sensory
 380 conditions, because different groups of subjects were tested for the two modalities.

381

382 Results

383 Experiment 1: Haptic and Visual Perception

384 Figure 5A shows that for the six geometric configurations of the squaring task (see methods) the
 385 subjects made systematic errors in both visual and haptic conditions. The comparison of the errors
 386 made using haptic information alone versus visual information alone shows consistent, opposing
 387 results for the two sensory modalities. Hence, in each task, when subjects made on average
 388 significant positive errors in the haptic condition, they made negative errors in the visual
 389 condition, and vice versa. Figure 5B represents the more robust evaluation of the errors obtained
 390 by considering the constraints existing between the errors performed in the six squaring tasks
 391 (see Methods, equations 1-3). The amplitude of the error was significantly different from zero for
 392 both visual and haptic perception in the Sagittal (visual: $F_{(17)}=5.86$, $p<10^{-4}$, haptic: $F_{(17)}=-8.10$, $p<10^{-6}$)
 393 and Transversal plane (visual: $F_{(17)}=-7.22$, $p<10^{-5}$, haptic: $F_{(17)}=9.22$, $p<10^{-6}$), but in the Frontal
 394 plane neither modality was significantly different from zero (visual: $F_{(17)}=-1.26$, $p=0.22$, haptic
 395 $F_{(17)}=-0.57$, $p=0.58$). Sensory modality had a significant effect in the Sagittal ($F_{(1,17)}=60.8$, $p<10^{-5}$)

and Transversal ($F_{(1,17)}=94.96$, $p<10^{-6}$) planes, but not in the Frontal plane ($F_{(1,17)}=0.14$, $p=0.71$). Remarkably, the significant perceptive errors in the Sagittal and Transversal planes had opposite sign between the two sensory conditions: when using haptic sense, subjects produced rectangles with the Anterior-Posterior dimension smaller than the Longitudinal and Lateral dimension, while, when using vision, they made rectangles with the Anterior-Posterior dimension larger than the Longitudinal and Lateral dimension. Moreover, when looking at the individual error in Figure 5C a strong (negative) correlation can be observed between visual and haptic errors ($R=-0.79$, $p<10^{-12}$), showing a clear relationship between the two, meaning that subjects who showed a stronger distortion in the visual domain also showed a stronger distortion, but in the opposite direction, in the haptic domain. The correlation remained significant when the average error in each plane was subtracted from the corresponding individual values (insert of Figure 5C, $R=-0.28$, $p<0.05$).

The vectorial representation of the individual errors for the two sensory modalities in Figure 5D fall along the same axis, but in opposite directions, meaning that the perceptual errors were in both cases restricted to an expansion (haptic) or contraction (visual) along the antero-posterior axis with little or no distortion in the fronto-parallel plane. The pattern of errors for the two modalities appear therefore complementary, in that they would tend to mutually cancel out when combined. Consistently, the analysis of cross-product between the haptic and visual individual vectors does not reveal any significant misalignment ($Mis=-52\pm55\text{mm}^2$, signed test: $p=0.48$). The angle θ between the average visual and haptic vector is $172\pm6^\circ$ and not significantly different from 180° (bootstrap $p=0.07$). Taking into account all possible orientations for the two groups of vectors, the observed results are 9 times more likely under the hypothesis that pattern of errors of the two senses are complementary ($H_0: \theta=180^\circ$), than under the alternative hypothesis (H_1), i.e. $\theta\neq180^\circ$. The average visual and haptic vectors show, on the other hand, amplitudes that are significantly different (bootstrap: $\Delta Amp=5.8\pm2\text{ mm}$ $p=0.003$), meaning that, although the pattern of errors for the two modalities are complementary, they would not exactly cancel each other out, although the difference would be small. The illustration of the 'perceptive cuboids' corresponding to the two sensory modalities reported in Figure 5E confirms that the haptic and

424 visual perceptive errors would mainly consist of a depth overestimation and underestimation for
425 the haptic and visual sense, respectively.

426 Even though the amplitude of the perceptive biases (constant components of the errors reported
427 in Figure 5) appear smaller for the haptic than for the visual modality, the latter is characterized
428 by a clearly smaller intra-personal variability of the responses ($\sigma_{\text{hapt}}=6.1\pm2.6$ mm, $\sigma_{\text{vis}}=4.2\pm2.2$ mm,
429 sensory modality effect: $F_{(1,17)}=12.02$, $p<10^{-2}$), corresponding to a higher precision for the visual
430 than for the haptic task.

431

432 [Figure 5 about here]

433

434 In summary, Experiment 1 shows clear differences in the patterns of visual and haptic distortions.
435 For both modalities the errors appeared primarily in the sagittal and transversal planes, and
436 amplitude and sign of the errors in one modality depended on amplitude and sign of the errors in
437 the other modality. More precisely, the pattern errors were opposite (contraction and expansion
438 of perceived depth for visual and haptic, respectively).

439

440 **Experiment 2: Effect of Body Orientation**

441 The responses of the subjects upright were characterized by constant errors similar to those
442 observed in Experiment 1 (Experiment effect: Wilks' Lambda=0.85, $F_{(4,32)}=1.35$, $p=0.27$). The left
443 columns of Table 3 and left panels of Figure 6 show that for both haptic and visual experiments
444 the squaring error appears consistent between postures if expressed egocentrically: we observed
445 no statistically significant effects of posture on the errors for any of the three planes when
446 expressed in body-centered reference frame. The misalignment, Mis , between the individual
447 vectors corresponding to upright and supine conditions (lower-left part of Figure 6A and 6B) is
448 not significantly different from zero (haptic: $Mis=20\pm47$ mm², signed test $p=0.81$; vision:
449 $Mis=2\pm12$ mm², signed test: $p=1$). For both sensory modalities, the difference in amplitude and
450 direction between average vector representing the pattern of errors in the upright and supine

position do not differ significantly from zero (bootstrap for haptics: $\Delta Amp=0.1\pm1.1$ mm $p=0.56$, $\theta=6\pm14^\circ$ $p=0.33$, $R_{0/1}=9.3$; bootstrap for vision: $\Delta Amp=-2\pm1.5$ mm $p=0.09$, $\theta=2\pm3^\circ$ $p=0.25$; $R_{0/1}=38$).

On the other hand, if the errors are represented in terms of allocentrically defined planes, i.e. fixed with respect to gravity (last three columns of Table 3 and right panels of Figure 6), a clear effect of posture can be observed in all planes for both sensory modalities on the orientation of the pattern of errors with significant misalignments: haptic $Mis=38\pm19\text{mm}^2$ signed test: $p=0.007$; vision: $Mis=109\pm55\text{mm}^2$ signed test: $p=0.001$). Consistently, the angle between the average vectors representing the errors in the allocentric space for the two postures is significantly different for both modalities: bootstrap $p<10^{-4}$ for haptics and vision.

460

[Figure 6 about here]

[Table 3 about here]

463

464

The intra-personal variability of the responses was not affected by the posture for the haptic modality ($\sigma_{\text{upright}}=6.2\pm6.1$ mm, $\sigma_{\text{supine}}=6.6\pm6.0$ mm, posture effect: $F_{(1,17)}=0.12$, $p=0.73$), but significantly increased in the supine position for the visual experiment ($\sigma_{\text{upright}}=3.5\pm3.2$ mm, $\sigma_{\text{supine}}=4.8\pm4.7$ mm, posture effect: $F_{(1,17)}=6.81$, $p=0.02$).

In conclusion, in this experiment we found that patterns of errors of both visual and haptic perception were invariant when expressed in an egocentric reference frame, but not when expressed in an allocentric one.

Experiment 3: Gravity's Effect on Visual and Haptic Perception

While the visual inputs are not different on ground and in weightlessness, the forces exerted against the virtual constraints during haptic exploration might be different in 0G due to biomechanical and neurophysiological effects. We therefore first analyze the changes in the contact forces between the subject's hand and the virtual object and then the pattern of squaring errors (Figure 7A-C). The left plot of Figure 7A shows that vertical forces applied by the subjects

on the upper and lower edge of the sensed object were modulated ($F_{(2,34)}=3.9$, $p=0.02$) by the experimental conditions (1G, 0G, Supported). As expected, upward and downward forces increased and decreased respectively in microgravity (post-hoc 1G Vs 0G, $p=0.02$), coherent with a reduction of the weight of the upper limb. When the weight of the arm was supported (see methods), the vertical forces also tended to differ from 1G condition (post-hoc Supp Vs 1G $p=0.09$) and were modulated in the same direction as in 0G (post-hoc Supp Vs 0G, $p=0.29$). Horizontal forces were also significantly affected by the experimental condition ($F_{(2,34)}=6.32$, $p<0.01$; Figure 7A, right plot), with a significant increase of the contact forces in microgravity with respect to the 1G and Support conditions.

This increase of the contact force in 0G, similar to what was previously observed in haptic tests during parabolic flights (Mierau et al., 2008), could be the result of a specific strategy aimed at keeping muscular tension, and hence muscle spindle sensitivity, similar to normal gravity conditions. This strategy would avoid the decrease in proprioception precision previously observed in weightlessness for 'open-chain' motor tasks, for which the same strategy could not be adopted, resulting in a decrease in muscle tension (Clément and Reschke, 2010). This hypothesis well matches the fact that the precision of haptic responses was not significantly affected by the experimental condition (response variability: 1G 6.8 ± 2.6 , 0G 7.1 ± 3.1 , Sup 6.4 ± 2.9 ; $F_{(2,34)}=1.75$, $p=0.19$), suggesting that neither microgravity nor the arm support significantly interfered with the subjects' ability to perform the task. This lack of microgravity effect on haptic precision appears in line with the results of previous orbital experiments (McIntyre and Lipshits, 2008).

Importantly, the results about the vertical contact forces and responses' variability suggest that the 'arm support' condition successfully mimicked the expected lightening of the arm observed in microgravity. Therefore, if haptic perceptive distortions (constant errors) are affected by microgravity, but not by the arm support, they would not be directly ascribable to the biomechanical action of microgravity on the arm.

504

[Figure 7 about here]

507 The comparison of the constant errors in the three experimental conditions, reported in Figure
 508 7B, clearly shows that the perceptive distortion characterizing haptic perception in the Sagittal
 509 plane was significantly amplified (became more negative) by microgravity, but was not affected
 510 by the arm support (condition effect $F_{(2,34)}=12.49$, $p<10^{-4}$), suggesting a perceptive rather than
 511 biomechanical effect. Similarly, the haptic distortion in the Transversal plane was amplified
 512 (became more positive) in 0G and was not affected by the support, either (condition effect
 513 $F_{(2,34)}=11.13$, $p<10^{-3}$). Finally, the lack of distortion in the Frontal plane persisted independent of
 514 the gravitational and support condition ($F_{(2,34)}=0.33$, $p=0.71$). Figure 7C shows a clear increase of
 515 the amplitude of average error vector in 0G (bootstrap: $\Delta Amp=5\pm1$ mm, $p<10^{-4}$). A nonsignificant
 516 misalignment between the haptic individual errors in the two gravitational conditions is reported
 517 ($Mis=2\pm33$ mm², signed test $p=1$) and consistently, the angle θ between the two average vectors
 518 is not significantly different from 0 (bootstrap $-5\pm16^\circ$ $p=0.62$; $R_{0/1}=8.4$).

519 For the visual tasks, Figure 7D shows that, as for the haptic sense, microgravity significantly
 520 modulated the perceptive distortions. More precisely, the large errors characterizing both sagittal
 521 and transversal planes in 1G were significantly reduced in weightlessness ($F_{(1,17)}=15.41$, $p=0.0011$
 522 and $F_{(1,17)}=7.87$, $p=0.012$ respectively). In the frontal plane, a small but significant height
 523 underestimation appeared in 0G ($F_{(1,17)}=9.531$, $p=0.007$). The polar plot of Figure 7E shows that
 524 the amplitude of the average error vector decreases in microgravity (bootstrap $\Delta Amp=-2.8\pm0.8$
 525 $p<10^{-4}$). Note that there is a small but significant misalignment between the 1G and 0G vectors
 526 ($Mis=16\pm12$, signed test $p=0.007$, bootstrap $\theta=7\pm3^\circ$ $p<10^{-4}$). The analysis of the variable component
 527 of the errors shows that microgravity did not significantly affect subjects' visual precision
 528 ($F_{(1,17)}=4.3$, $p=0.054$), although the response variability tended to increase from 4.4 ± 2.5 to 5.2 ± 2.4
 529 mm.

530 The qualitative comparison of Figure 7F and Figure 7G illustrates that the effect of gravity on
 531 both sensory modalities mainly consists of a stretch of depth perception with respect to normo-
 532 gravity conditions (an increase in slenderness for haptic; a decrease in stubbiness for visual).

533 In neither haptic nor visual 0G tasks did the amplitude of the errors appear to change over the
534 parabolas (trial number effect on haptic errors: Sagittal $F_{(4,60)}=0.79$, $p=0.54$; Transversal $F_{(4,60)}=0.23$,
535 $p=0.92$; Frontal $F_{(4,60)}=0.49$, $p=0.74$; and on visual errors Sagittal $F_{(4,68)}=1.23$, $p=0.30$; Transversal
536 $F_{(4,68)}=0.60$, $p=0.67$; Frontal $F_{(4,68)}=0.63$, $p=0.64$) suggesting a lack of significant adaptation to
537 microgravity during the experiment duration.

538 The direct quantitative comparison of the effect of microgravity, $\Delta\bar{\epsilon}_s$, between the two groups of
539 subjects of the visual and haptic experiments (Figure 8A) shows similar modulations of the
540 perceptual distortion for both senses (Wilks' Lambda=0.91, $F_{(3,32)}=0.96$, $p=0.42$). Although
541 the amplitude of the microgravity effect tends to be larger for haptic than for visual perception
542 (bootstrap, $p=0.06$), the average directions of the microgravity effect on visual and haptic
543 sense appear very similar (Figure 8B): the angle θ between the two vectors representing
544 the average effect of gravity on the two modalities is only $15.6\pm 15.6^\circ$ and not significantly
545 larger than zero (bootstrap, $p=0.14$). When considering the range of all possible θ ($\pm 180^\circ$),
546 Bayesian statistics suggest that the observed data are 5.2 times more likely under the
547 hypothesis that $\theta=0^\circ$ (H_0) than under the hypothesis $\theta\neq 0^\circ$ (H_1). As shown in Figure 7B and
548 7D, the perceptive error predicted in 0G, $\hat{\epsilon}_{s,0G}$, by assuming that the gravity effect is identical for
549 the haptic and visual modality (both in terms of direction and amplitude) are indeed
550 indistinguishable from the observed results (Wilks' Lambda=0.73, $F_{(6,12)}=0.73$, $p=0.63$), despite the
551 small difference in orientation between $\Delta\epsilon_{visual}$ and $\Delta\epsilon_{haptic}$ and despite the slight change in
552 orientation of the visual vector when passing from 1G to 0G (see above).

553

554 [Figure 8 about here]

555

556 To summarize, the parabolic flight experiments show that, although opposite perceptive errors
557 characterize vision and haptic sense in normal gravity conditions, the effects of microgravity on
558 each of those patterns of errors are in the same direction for the two sensory modalities.

559 Results Summary

560 Experiment 1 revealed strong, complementary distortions between haptic and visual perception
561 of 3D geometry. Subjects visually underestimated an object's depth with respect to both height

562 and width, whilst overestimating depth when exploring the object haptically. In Experiment 2
563 the comparison of seated versus supine body orientation clearly showed that both visual and
564 haptic distortions align with the subject's body rather than with gravity. Experiment 3, conducted
565 during parabolic flight, showed a clear effect of microgravity on both haptic and visual distortion.
566 Importantly, despite the fact that the perceptive errors in normo-gravity were in the opposite
567 directions for visual and haptic tasks, the changes induced by microgravity were in the same
568 direction along the anterior-posterior axis: weightlessness increases the haptic over-estimation of
569 depth with respect to width and height and decreases the visual under-estimation of depth with
570 respect to width and height.

571 **Discussion**

572 The experiments presented here aimed to understand how gravity affects the perception of 3D
573 shapes. We extend previous studies restricted to vision to include haptic sensation, by using the
574 same experimental paradigm for the two modalities. In the following we argue for a modality-
575 independent role of gravity in interpreting incoming sensory signals.

576 **Haptic and Visual perception in normo-gravity conditions**

577 Individually, the visual and haptic distortions observed here are consistent with previous findings
578 obtained without using head-mounted displays or haptic devices, supporting the validity of the
579 present experimental paradigms. Our haptic results concur with overestimation in the radial
580 dimension observed for haptic tasks (Lipshits et al., 1994; Armstrong and Marks, 1999; Fasse et
581 al., 2000; Henriques and Soetiching, 2003). Similarly, visual underestimation of depth has been
582 previously reported in the horizontal plane (Wagner, 1985; Loomis and Philbeck, 1999).
583 Surprisingly, we observed no significant 'horizontal-vertical illusion' previously observed in the
584 frontal plane (Avery and Day, 1969). Stimulus placement in front of the right shoulder in our
585 experiment, rather than straight ahead, may have impeded interpreting vertical and horizontal
586 lines as depth cues, which is purported to be the source of the illusion cited here (Girgus and
587 Coren, 1975).

588 Our experiments with supine subjects also show that the patterns of visual and haptic errors are
589 tied to the axes of the body, not to gravity. Although in apparent contradiction with the effects
590 of body tilt on visual tasks (Marendaz et al., 1993; Leone, 1998; Barnett-Cowan et al., 2015), or
591 external forces on haptic perception (Wydoodt et al., 2006), our observed posture-invariant error
592 pattern concurs with previously reported body-centered and eye-centered encoding of haptic
593 (Gurfinkel et al., 1993; Dupin et al., 2018) and visual information (Averly and Day, 1969; Howard
594 et al., 1990; McIntyre et al., 1997; Henriques et al., 1998; Vetter et al., 1999) and with the lack of
595 body-tilt effect in unimodal, but not cross-modal, tasks (Bernard-Espina et al., 2022).

596 Although perceptual biases are already known to differ between visually and haptically guided
597 pointing (vanBeers et al., 1999; Liu et al., 2018), we show for the first time a complementarity
598 and a negative correlation between the two. Although we cannot fully discard the hypothesis of
599 a fortuitous correspondence between modality-specific mechanisms, such as integration of eye
600 vergence signals for vision (Murdison et al., 2019) or exploratory movement kinematics for haptic
601 (Armstrong and Marks, 1999), our findings suggest some level of shared neural processing. In
602 previous studies, the sequential nature of haptic shape exploration, requiring information storage
603 in working memory, was shown to contribute to perceptive distortions (McFarland & Soechting,
604 2007). Similarly, both pointing to memorized targets (McIntyre et al., 1998) and haptic-visual
605 comparisons (McIntyre and Lipshits, 2008) showed distortions related to memory storage and
606 coordinate transformations. The sequential nature of the haptic explorations in our experiments,
607 and the likely need for sequential visual scanning, plus the need to compare lengths along
608 different directions, would require similar central processing of spatial information. The clearly
609 different distortions in visual versus haptic suggests that these tasks are carried out by separate,
610 modality-specific processes. Nevertheless, the link between modality-specific squaring errors
611 reported here suggests that central neural processes associated with memory storage and
612 coordinate transformations are shared between the two.

613

614 **3D object perception in microgravity**

615 Although the egocentric patterns observed for visual and haptic errors would suggest that an
616 external cue, such as gravity, should not influence shape perception, the strong microgravity
617 effects observed in parabolic-flight clearly show the contrary. How can these apparently
618 contradictory results be reconciled? We have shown that the observed effects of microgravity on
619 both haptic and visual perceptive distortions are not directly ascribable to a decrease in their
620 precision, nor to the mechanical action of gravity on the arm in the haptic task (arm support and
621 supine conditions). Moreover, the remarkable similarity between microgravity's effects on visual
622 and haptic distortions makes it unlikely that they are caused by independent effects on the two
623 sensory systems, such as modifications of proprioceptive-tactile receptors' output for haptic tasks
624 (Lipshits et al., 1994) or alterations of eye movement control for visual tests (Clement et al., 1989;
625 Clarke et al., 2013). A more parsimonious and likely explanation is an effect of gravity on sensory
626 processing that is shared by the two sensory modalities, which could be only hypothesized in
627 previous unimodal studies (Clement et al. 2009, 2012, 2013).

628 **Through what mechanism does gravity affect shape perception?**

629 The observed modality-independent effects of gravity on shape perception can be associated to
630 vestibular/otolithic projections toward the neural-network that recurrently connect the brain
631 areas involved in the haptic and visual representation of objects and whose existence has been
632 revealed by various brain imaging and electrophysiological studies (Figure 9A). The Lateral
633 Occipital Complex (LOC), known to be activated by 3D object images, is also active during haptic
634 shape recognition. Similarly, S1, S2, vPM and BA5 areas, commonly associated with haptic object
635 perception are activated also by images of manipulable objects. These cross-modal activations are
636 mediated by the intraparietal sulcus (IPS), whose activity is enhanced during cross-modal, visuo-
637 haptic object recognition. That IPS plays a role in reconstructing a visual representation of a
638 haptically sensed object, and vice versa, is supported by electrophysiological activity consistent
639 with recurrent neural networks able to perform cross-modal sensory re-encoding (Pouget et al.,
640 2002; Avillac et al., 2005). The coexistence of visual and haptic object representations, as depicted
641 in Figure 9B, is consistent with behaviourally observed concurrent representations of

642 reaching/grasping tasks (McGuire and Sabes, 2009, 2011; Tagliabue and McIntyre, 2011-2014)
643 and with the link that we observed here between haptic and visual perceptive errors in normo-
644 gravity conditions.

645 [Figure 9 about here]

646 We propose the trans-modal processing performed by IPS, as depicted in Figure 9, as the source
647 of the modality-independent distortions observed when performing the experiment in 0G. To
648 transform a visually-acquired object into a stable haptic representation (and vice versa), despite
649 potential independent movements of the two sensory systems, the IPS network must use a stable
650 internal representation of the body and/or peripersonal space (Andersen et al., 1997; Cohen and
651 Andersen, 2002; Land, 2014), built by constantly integrating signals about the eye-hand
652 kinematic chain and the body position in space, including vestibular inputs. Clear evidence that
653 internal models of body/space affect the interpretation of incoming sensory information in a
654 Bayesian fashion has been extensively reported, e.g. the ‘Ames room’ and the Müller-Lyer visual
655 illusions being based on prior knowledge about the geometry of constructed environments
656 (O'Reilly et al., 2012) or the cutaneous Rabbit illusion (Goldreich et al., 2007). The contribution
657 of gravitational signal to the body/space representation concurs with a) vestibular (i.e. otolithic)
658 projections to IPS-area reported in numerous electrophysiological studies (Blanke et al., 2000;
659 Miyamoto et al., 2007; Schlindwein et al., 2008; Chen et al., 2011, 2013), b) the observed
660 interference of head-tilt with the re-encoding of sensory signals between visual and haptic space
661 (Tagliabue and McIntyre, 2011, 2013; Burns et al., 2011; Bernard-Espina et al., 2022) and c) the
662 effect of vestibular stimulation on self-body-size perception (Mast et al., 2014).

663 The similar effect of microgravity on both visual and haptic object perception observed here could
664 hence be explained by a deformation of the body schema and/or internal representation of the
665 peripersonal 3D space due to the unusual lack of gravity. Indeed, IPS recurrent neural network
666 connections are set/learnt for working in the presence of tonic, gravity-dependent, otolithic
667 inputs. If the network lacks this input, without appropriate adjustments to the synaptic weights,
668 the cross-modal transformations, and thus the concurrent object representations, would be
669 inexorably and similarly affected. In experiments studying visual perception in microgravity it
670 was indeed observed that distortions of object size perception are accompanied by a modification

671 of the subjective eye height estimation (Clement et al., 2008, 2013; Burrelly et al., 2015-2016),
672 that, in the light of our hypothesis, would reflect a distortion of the internal representation of the
673 body and/or peripersonal space.

674 **Conclusions**

675 Our study offers a better understanding of human perception of 3D geometry. We have provided
676 evidence for separate, modality-specific representations for visual and haptic object perception
677 in our tasks. Nevertheless, the observed link between the errors characterizing the two senses,
678 together with recent findings about reciprocal activations of the visual and haptic cortical
679 systems, indicate a tight interaction between concurrent visual and haptic object representations.
680 Furthermore, the observation that microgravity has the same incremental effect on visual and
681 haptic object perception argues for a modality-independent perceptive mechanism. Via this
682 mechanism, modality-specific object information would be treated by neural networks of the
683 parietal cortex and interpreted through an internal representation of the body and egocentric 3D
684 space, shaped by gravity (otolithic) signals. These microgravity experiments, therefore, provide
685 fundamental cues to better understand the neurophysiology of perception on Earth. They suggest
686 that fully independent, modality-specific 3D object perception does not exist, as the modalities
687 are inexorably linked by gravity. This implies that restricting future investigations to the brain
688 areas associated with a single sensory modality, even when studying only a modality-specific
689 behavior, would be a clear limiting factor in understanding the neural mechanisms underlying
690 3D object perception.

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Figure Legends

Figure 1: A) Haptic device and virtual reality headset used for the haptic and visual experiments, respectively. In panels B) and C) are reported the name of the orthogonal directions defined in an egocentric, body-centered (Longitudinal, LO; Lateral, LA; Anterior-Posterior, AP) and external, gravity-centered (Up-Down, UD; East-West, EW; North-South, NS) reference frames respectively. The bottom part of the figure represents the planes in which the task is performed expressed in the body-centered (Transversal, Sagittal and Frontal) and gravity-centered (Horizontal, Meridian and Latitudinal) reference frames.

Figure 2: Geometrical configurations of the task. The first row represents the six geometric configurations, which correspond to the combination of the three planes in which the rectangle could lie and the two different dimensions of the rectangle that the subject had to adjust. For each combination of geometric configuration and postural conditions (Upright and Supine), the table reports with black bold text the anatomical (egocentric) plane in which the task is performed as well as the anatomical direction of the adjustable (Adj.) and reference (Ref.) dimensions of the rectangles. The gray text in the lower part of the table corresponds to the definitions, in a gravity-centered reference frame arbitrarily looking north, of the task planes, as well as of the adjustable and reference dimensions of each rectangle. These allocentric definitions are independent of the postural condition. These terms are useful to refer to the various planes when testing the hypotheses of egocentric versus allocentric distortions.

Figure 3: Sign conventions for the errors in the Transverse, Frontal and Sagittal planes. The gray squares represent the correct answer (i.e. a square). The black lines represent the distorted answers. Positive planar error values correspond to “stubby” rectangles. Negative values correspond to “slender” rectangles. The same conventions are used for the error expressed in the allocentered planes. In this case, North-South (NS), East-West (EW) and Up-Down (UD) directions replace Anterior-Posterior (AP), Lateral (LA) and Longitudinal (LO), respectively. Horizontal, Latitudinal and Meridian replace Transversal, Frontal and Sagittal planes, respectively.

Figure 4: Method used for data filtering and for their vectorial representations. **A)** Fictitious individual errors recorded for the squaring task in the three anatomical planes (Sagittal, Transversal and Frontal) with the corresponding filtered value (see following panel). **B)** Each triplet of measured errors is represented as a point in a 3D space. The errors in the three anatomical planes should theoretically fulfill the constraint described by equation 3, corresponding to the solution plane represented in gray. The 3D point (black dot) is

hence projected on the solution plane (blue dot), removing the inconsistent components of the recorded errors. The three components of the projection (blue dot) are then used for the representation of the data in terms of the three planar error (filtered error in the first panel) and for the polar plot representation reported in the third panel. **C)** To improve readability, the data projected on the solution plane are reported as 2D polar plot, where the error triplets are represented as 2D vectors. In panels B-C the discontinuous lines represent the locations of triplets of errors lying in the solution plane and characterized by the following additional relationships: $\bar{\epsilon}_{Fro} = 0$ and hence $\bar{\epsilon}_{Sag} = -\bar{\epsilon}_{Tra}$ (dot-dashed line); $\bar{\epsilon}_{Tra} = 0$ and thus $\bar{\epsilon}_{Sag} = \bar{\epsilon}_{Fro}$ (dotted line); $\bar{\epsilon}_{Sag} = 0$ and $\bar{\epsilon}_{Tra} = \bar{\epsilon}_{Fro}$ (dashed line). The center of the polar plot corresponds to null errors in all three planes. **D)** Graphical representation of the 'Mis' parameter used to quantify the misalignment between two individual vectors and corresponding to the gray area of the parallelogram having the two vectors as sides.

Figure 5: **A)** Errors for the task performed in each of the six geometrical conditions using haptic information only (light blue bars) or visual information only (red bars). Each geometrical condition is characterized by the plane in which the rectangle lies (sagittal, transversal, frontal), and by which direction within the plane was adjustable or held constant: Longitudinal (Lo), Anterior-Posterior (AP), and Lateral (La). Positive errors correspond to the final size of the adjustable dimension being greater than the reference dimension. Vertical whiskers represent 95% confidence intervals. A significant difference between the two tasks performed in the same plane is indicative of an important perceptive distortion in that specific plane. **B)** Perceptive errors in the three task planes for haptic and visual conditions. *** : $p < 10^{-3}$ in the ANOVA testing the modality effect. ‡ : $p < 10^{-3}$ for the t-test ascertaining differences from zero. **C)** Individual planar errors in the visual tasks as function of the errors in the haptic tasks. Each marker type corresponds to a specific subject. Their level of gray represents the plane of the task (black=sagittal, light-gray=frontal, dark-gray=transvers). The dashed line represents the data linear regression. The top-right insert represents the same data after subtracting to each point the mean error of the corresponding task plane. **D)** Vectorial representation of participant errors. Thicker vectors correspond to the vectorial average of the individual responses (thinner vectors). For details about the meaning of the polar plot representation see Figure 4C. **E)** Perceptive cuboids illustrating of how a cube (gray shape) would be perceived by the subjects when using haptic or visual information alone, respectively. For illustration purposes, the distortions of this panel are scaled up by a factor of 5. Data reported in all panels are based on the performances of 18 subjects.

Figure 6: Errors within each plane when the subjects are seated normally (Upright) or lying Supine. The upper **(A)** and lower **(B)** panels represent the results for the Haptic and Visual modalities, respectively. The left panels represent the errors per anatomical, egocentric plane. The right panels represent the data per

allocentric (fixed with respect to gravity) plane. **: $p < 10^{-2}$ and ***: $p < 10^{-3}$ in the ANOVA. † and ‡ : $p < 10^{-2}$ and $p < 10^{-3}$ for the t-test ascertaining differences from zero. Vertical whiskers represent 95% confidence intervals. In each barplot the inset reports the perceptive cuboids corresponding to the 3D perceptive distortion (amplified x5) of a cube. The polar plots report the vectorial representation of the individual errors. Thicker vectors represent the average vectorial response. For details about the meaning of the polar plot representation see Figure 4C. Data reported in this figure are based on the performances of 36 subjects (18 for haptic and 18 for visual experiment).

*Figure 7: Results of the microgravity experiments for the haptic (A-C and F panels) and visual (D-E and G panels) tasks. A) Contact forces in the three experimental conditions: normogravity (1G), microgravity (0G) and with a mechanical support of the arm (Supp). Left: Vertical forces generated against the upper and lower edges of the rectangle. Right: Horizontal forces generated against all other edges of the rectangle. B) and D) Errors observed in the three task planes for each experimental condition, together with the error predicted in microgravity assuming the same effect of gravity on both haptic and visual tasks. C) and E) are polar plots representing individual errors. Thicker vectors represent the average vectorial response. For details about the meaning of the polar plot representation see Figure 4C. F-G) Illustration of the perceptive cuboids (experimental results scaled up by 5) in normal gravity and in microgravity together with the reference cube (gray). *: $p < 0.05$, **: $p < 10^{-2}$ and ***: $p < 10^{-3}$ in the ANOVA. †, ‡ and ‡ : $p < 0.05$, $p < 10^{-2}$ and $p < 10^{-3}$ for the t-test ascertaining difference from zero. Data reported are based on the performances of 36 subjects: 18 for the haptic and 18 for the visual experiment.*

Figure 8: Comparison of the effect of microgravity on the Haptic and Visual senses. A) Difference between the constant errors made by the subjects in the 0G and 1G conditions for the tasks in the three anatomical planes. Vertical whiskers represent 95% confidence interval. B) Vectorial representation of the gravity effect. Thicker vectors represent the average response. For details about the meaning of the polar plot representation see Figure 4C. Data reported are based on the performances of 36 subjects (18 for the visual and 18 for the haptic experiment).

Figure 9: A) Evidences of neural activation associated to haptic (blue), visual (red) and cross-modal (orange) objects' perception. The regions primarily involved in haptic objects representation are the primary and secondary somatosensory areas (S1 and S2), the Brodmann area 5 (BA5), and the ventral premotor (vPM) area. The 3D object visual representation is known to reside in the lateral occipital complex (LOC). Numbers' font size qualitatively represents the intensity of the neural activation during object perception tasks: 1

Sakata et al. 1973; 2 Koch & Fuster 1989; 3 Moore & Engel 2001; 4 James et al. 2002; 5 Grefkes et al. 2002; 6 Amedi et al. 2002; 7 Grill-Spector 2003; 8 Deshpande et al. 2008; 9 Stilla & Sathian 2008; 10 Vingerhoets 2008; 11 Lacey et al. 2009; 12 Meyer et al. 2011; 13 Snow et al. 2014; 14 Sun et al. 2016; 15 Yau et al. 2016. Green letters represent studies reporting otolithic projection in the intraparietal sulcus (IPS) area: a Blanke et al. 2000; b Miyamoto et al. 2007; c Schlindwein et al. 2008; d-e Chen et al. 2011, 2013. **B)** Proposed schematic of information processing underlying objects perception. Space/body internal representations reciprocally connect concurrent haptic and visual object representation and allow building a visual representation of the object from haptic signals and vice versa. Otolithic signals affect the body/space internal representation, distorting both haptic and visual object representations. Beneath the blocs are reported their identified cortical location based on electrophysiological and brain imaging findings reported in the literature.

Table Legends

Table 1: Definition of the squaring errors for all six geometrical configurations of the task.

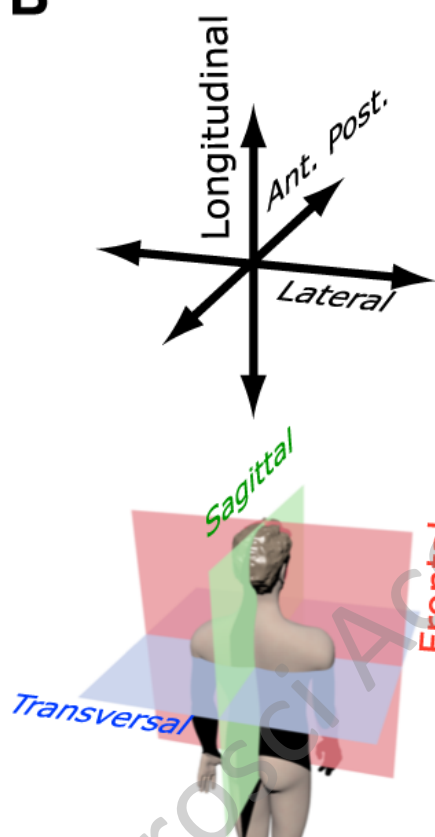
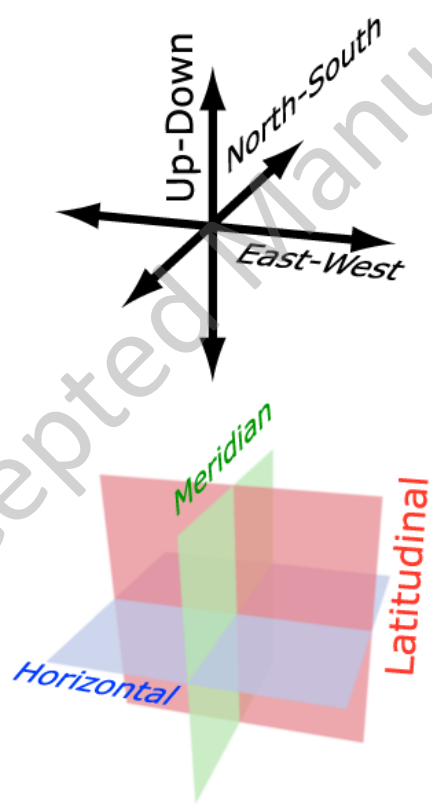
Plane	Adjustable dimension	Reference dimension	Task error
Frontal	LA	LO	$\varepsilon_{LA-LO} = \varepsilon_{LA} - \varepsilon_{LO}$
	LO	LA	$\varepsilon_{LO-LA} = \varepsilon_{LO} - \varepsilon_{LA}$
Transversal	LA	AP	$\varepsilon_{LA-AP} = \varepsilon_{LA} - \varepsilon_{AP}$
	AP	LA	$\varepsilon_{AP-LA} = \varepsilon_{AP} - \varepsilon_{LA}$
Sagittal	LO	AP	$\varepsilon_{LO-AP} = \varepsilon_{LO} - \varepsilon_{AP}$
	AP	LO	$\varepsilon_{AP-LO} = \varepsilon_{AP} - \varepsilon_{LO}$







Table 2: Relationship between ego- and allo- centrically defined distortions for the Upright and Supine condition.

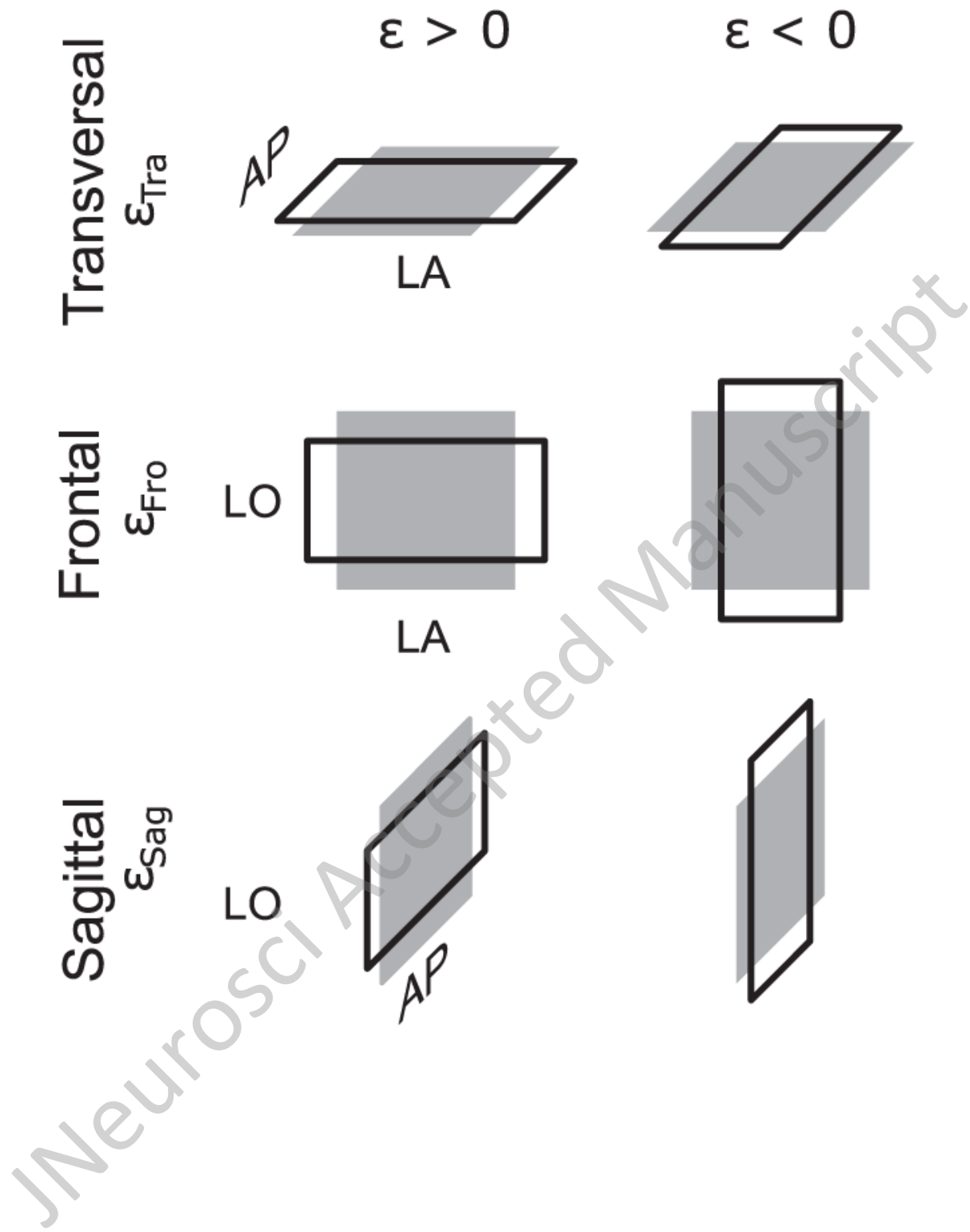
Upright	$\bar{\varepsilon}_{Mer} = \bar{\varepsilon}_{Sag}$	$\bar{\varepsilon}_{Lat} = \bar{\varepsilon}_{Fro}$	$\bar{\varepsilon}_{Hor} = \bar{\varepsilon}_{Tra}$
Supine	$\bar{\varepsilon}_{Mer} = -\bar{\varepsilon}_{Sag}$	$\bar{\varepsilon}_{Lat} = \bar{\varepsilon}_{Tra}$	$\bar{\varepsilon}_{Hor} = \bar{\varepsilon}_{Fro}$

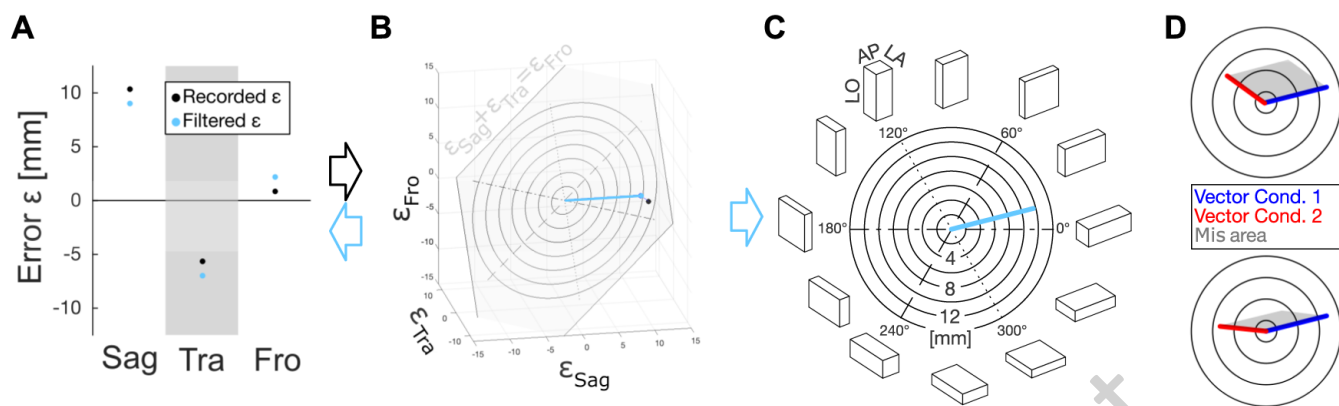
Table 3: Results of ANOVA for the posture effect on the planar perceptive distortion.

	Sagittal	Transversal	Frontal	Meridian	Horizontal	Latitudinal
Haptic	F(1,17)=0.40	F(1,17)=0.58	F(1,17)=0.001	F(1,17)=52.28	F(1,17)=13.01	F(1,17)=12.18
	p=0.53	p=0.46	p=0.97	p<10 ⁻⁵	p=0.002	p=0.003
Visual	F(1,17)=2.00	F(1,17)=1.32	F(1,17)=0.15	F(1,17)=25.46	F(1,17)=19.92	F(1,17)=22.87
	p=0.18	p=0.27	p=0.70	p<10 ⁻³	p<10 ⁻³	p<10 ⁻³

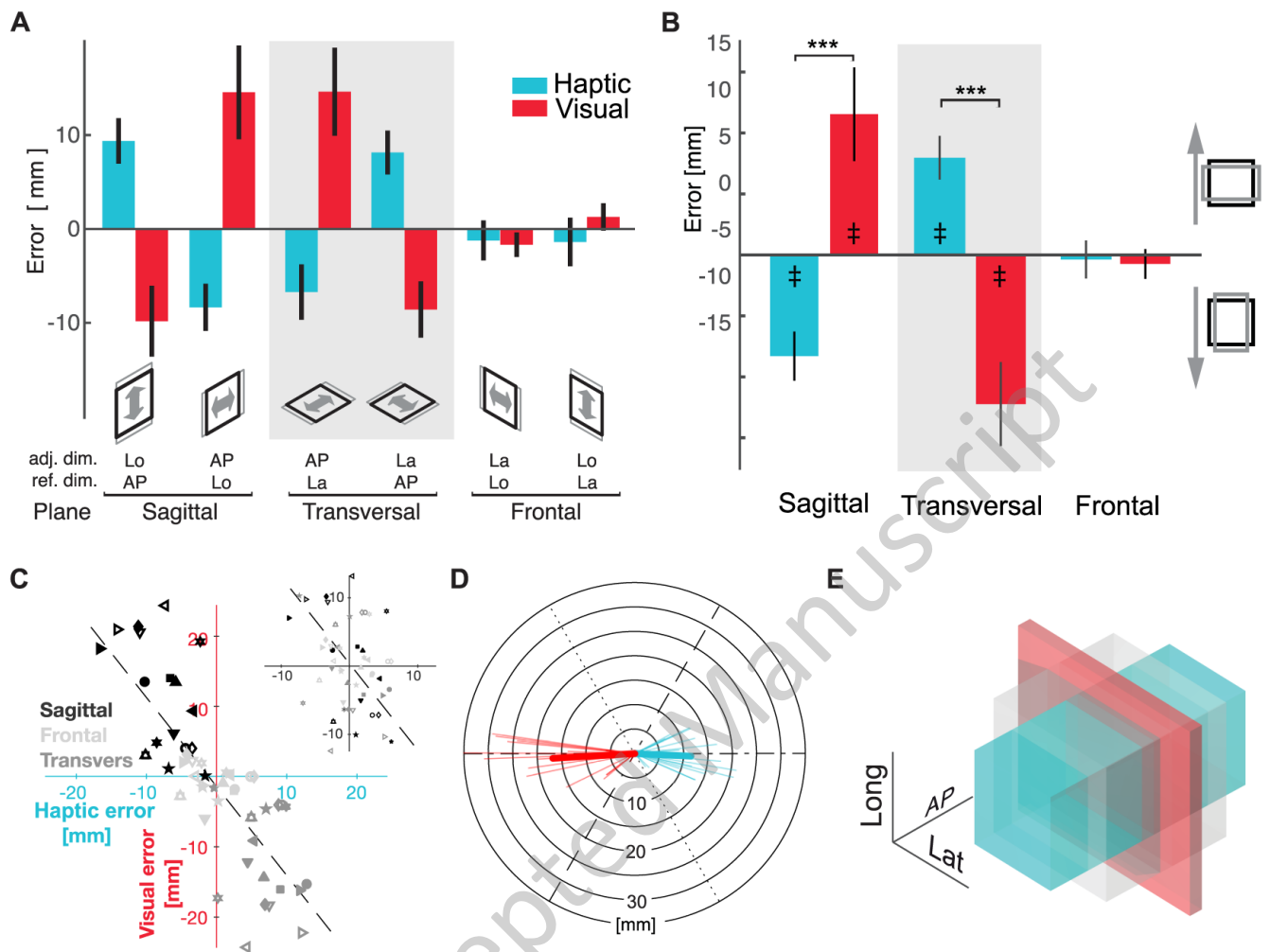
A**B****C**

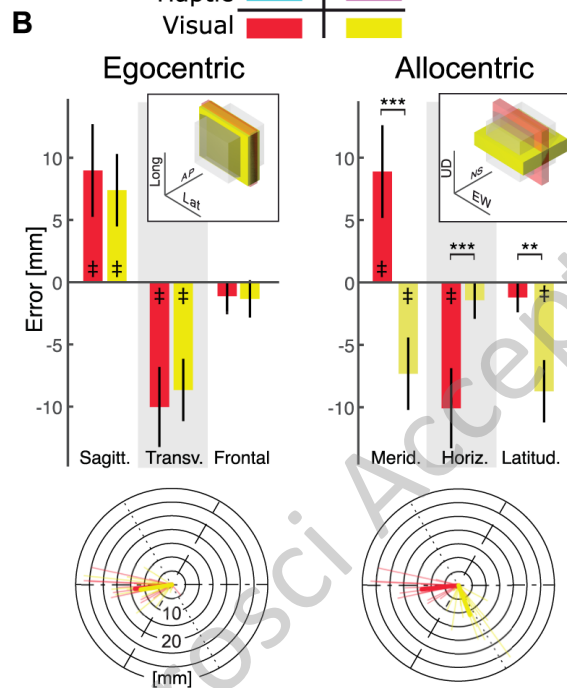
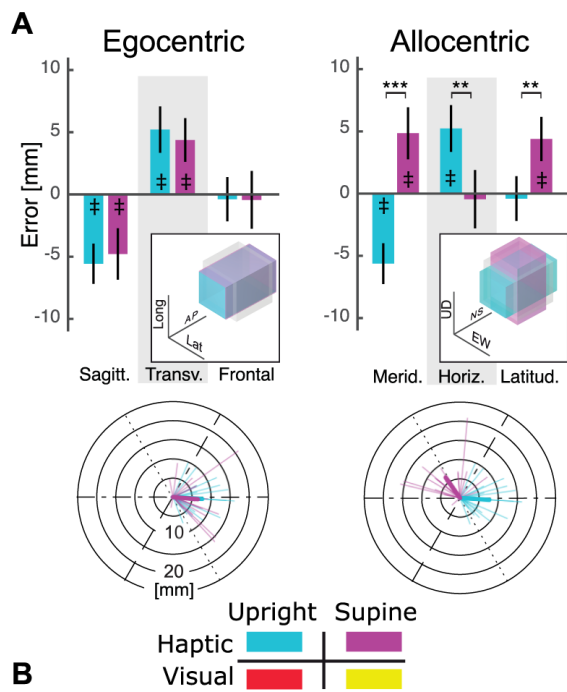
							
Upright	Plane	Frontal		Transversal		Sagittal	
	Adj. Dim.	Lateral	Longitudinal	Lateral	Ant-Post	Longitudinal	Ant-Post
	Ref. Dim.	Longitudinal	Lateral	Ant-Post	Lateral	Ant-Post	Longitudinal
Supine	Plane	Transversal		Frontal		Sagittal	
	Adj. Dim.	Lateral	Ant-Post	Lateral	Longitudinal	Ant-Post	Longitudinal
	Ref. Dim.	Ant-Post	Lateral	Longitudinal	Lateral	Longitudinal	Ant-Post
		Plane		Latitudinal		Horizontal	
						Meridian	
		Adj. Dim.	East-West	Up-Down	East-West	North-South	Up-Down
		Ref. Dim.	Up-Down	East-West	North-South	East-West	Up-Down

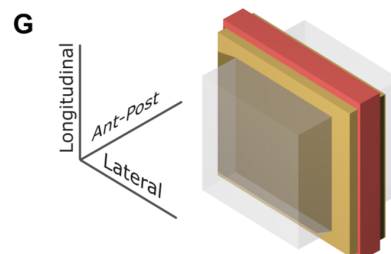
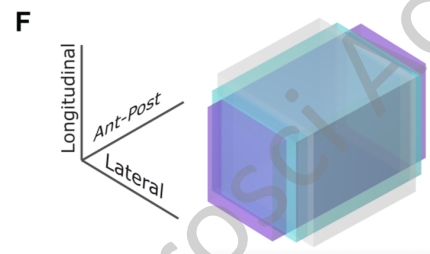
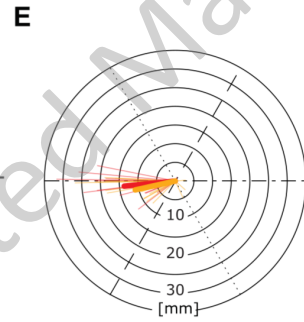
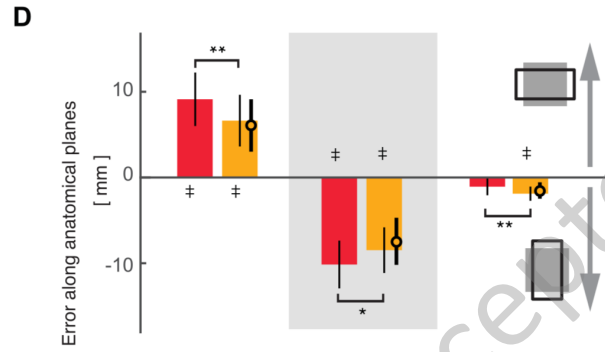
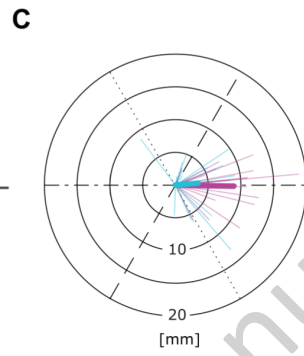
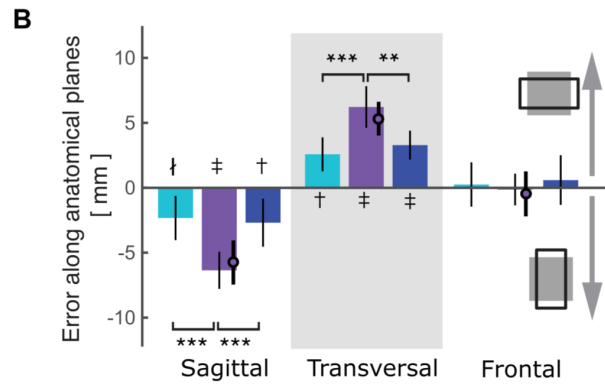
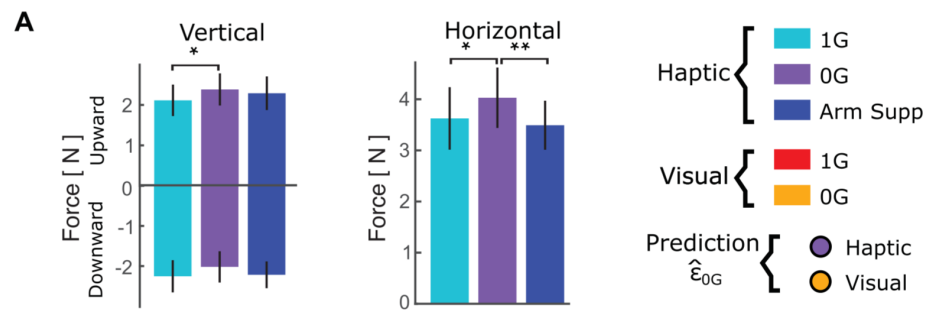


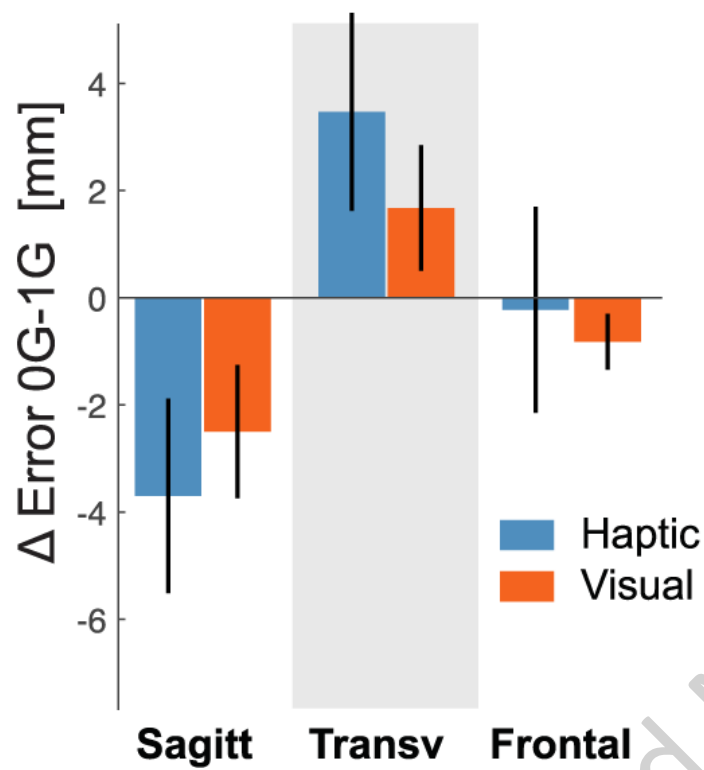
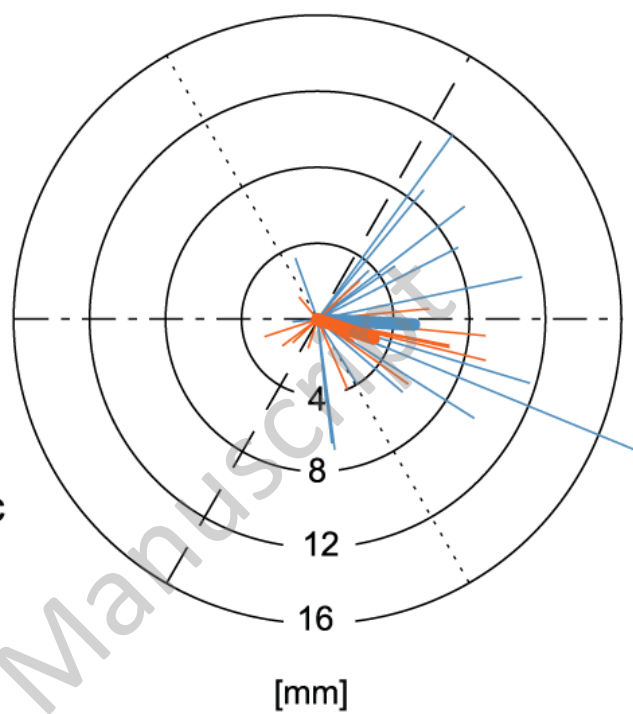


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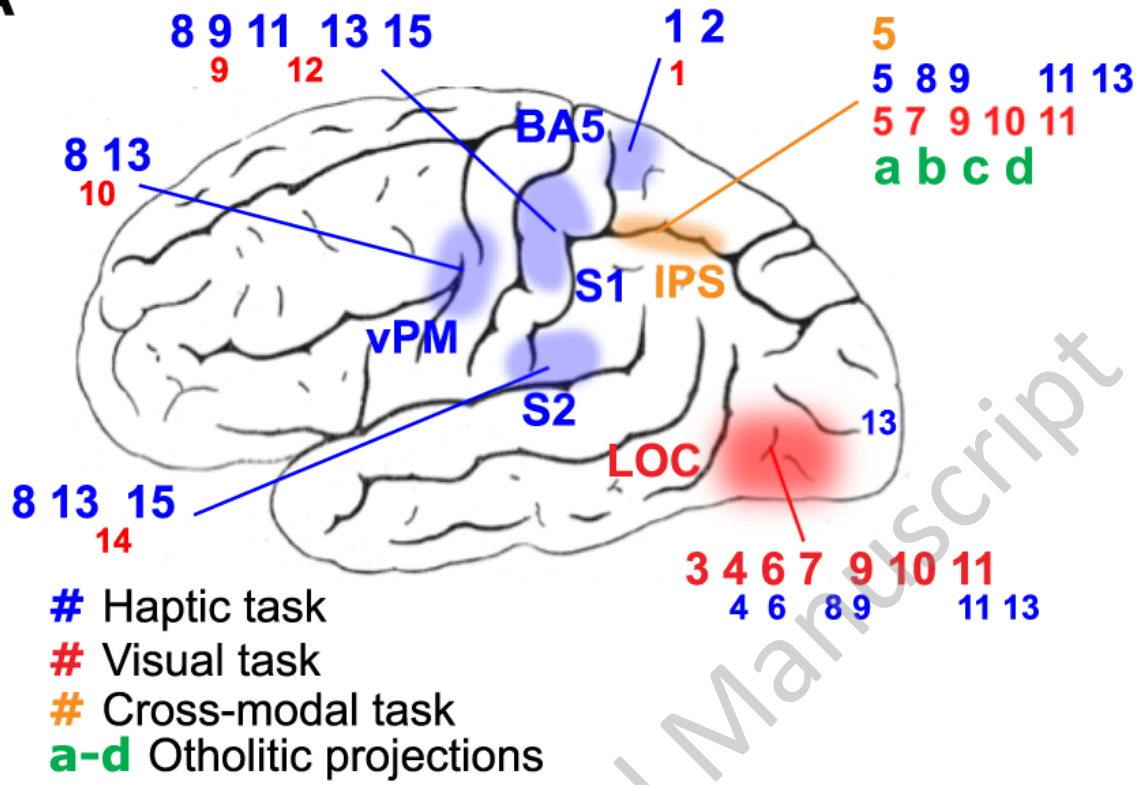






A**B**

A



B

